Revision of *Cricetodon soriae* (Rodentia, Mammalia), New Data from the Middle Aragonian (Middle Miocene) of the Calatayud-Daroca Basin (Zaragoza, Spain)

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ARTICLE

REVISION OF *CRICETODON SORIAE* (RODENTIA, MAMMALIA), NEW DATA FROM THE MIDDLE ARAGONIAN (MIDDLE MIOCENE) OF THE CALATAYUD-DAROCA BASIN (ZARAGOZA, SPAIN)

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ABSTRACT—The oldest record of *Cricetodon* (Cricetidae, Rodentia, Mammalia) from the Aragonian type area (Calatayud-Daroca Basin, Zaragoza, Spain) is described. The remains from Las Umbrías (LUM) and Las Planas (LP) sections are attributed to *Cricetodon soriae*, described in the locality Somosaguas N (SOMN) from the Madrid Basin (biozone E, MN5). The studied material (including 52 jugal teeth) belongs to eight localities spanning a time interval from 14.06 to 13.80 Ma, covering the entire biozone E. A morphometric analysis of the Calatayud-Daroca material provides the most specific and detailed descriptions of *C. soriae* until now. New complete descriptions of the type material from SOMN and an emended diagnosis of *C. soriae* are presented. Comparisons with all the species of *Cricetodon* described to date have been made. Differences between *Cricetodon aureus* and *Cricetodon meini* are discussed; the results yielded by the study of more than 100 upper third molars from Vieux-Collonges make it possible, for the first time, to distinguish between those of *C. aureus* and *C. meini*, and to compare them both with *C. soriae*. The presence of common characteristics indicates a closer relationship of *C. soriae* with the species of *Cricetodon* from Asia Minor than with the first representatives of *Cricetodon* in central and eastern Europe. The distribution of *C. soriae* in the Iberian Peninsula is coincident with the global cooling event and the increasing in aridity in southwestern Europe, and the faunal dispersion event called *Conohyus/Pliopitechus* that took place during the local biozone E.

INTRODUCTION

The Calatayud-Daroca Basin, situated in the northeastern part of the Iberian Peninsula (Fig. 1), is filled by a thick succession of continental deposits ranging from the Paleogene to the early Pliocene (Daams et al., 1999a). The stratigraphic superposition of the fossiliferous levels, and their abundance and richness of micromammal fossil remains, makes this basin interesting for the study of rodent evolution, biostratigraphy, and biochronology (Daams et al., 1998, 1999a). One of its stratigraphic sections is the stratotype of the Aragonian continental stage that constitutes the uppermost part of the lower Miocene and the entire middle Miocene (Daams et al., 1977, 1981). New discoveries in the Calatayud-Daroca Basin have allowed the detailed description of the Aragonian stage (Daams et al., 1999b; van der Meulen et al., 2012). The Aragonian type area has provided fossil remains that offer detailed information of rodent faunas (Álvarez-Sierra, 1987; Cuenca Bescós, 1988; de Bruijn and Saraç, 1992; García-Paredes, 2006; García-Paredes et al., 2009, 2010; Oliver et al., 2009; Peláez-Campomanes, 2001; van der Meulen et al., 2003, 2012). It is situated near Villafeliche, between Calatayud and Daroca villages (province of Zaragoza). It is composed of four sections: Vargas, Valdemoros, Las Umbrías, and Las Planas (Daams et al., 1999a). This study focuses on the older localities situated in Las Umbrías and Las Planas sections. The age estimation of the localities ranges from 14.06 to 13.80 Ma (van Dam et al., 2006), corresponding to the local biozone E (Daams et al., 1999b; Garcés et al., 2003; van der Meulen et al., 2012). This local biozone can be correlated to the upper part of the Neogene Mammal Zone MN5 (Daams et al., 1999a, 1999b; van der Meulen et al., 2012).

The species revised here belongs to the genus *Cricetodon* Lartet, 1851, a large rodent of the family Cricetidae. *Cricetodon* includes 22 fossil species; four of them are present in the Calatayud-Daroca Basin (Freudenthal, 1966; de Bruijn et al., 1993; López-Guerrero et al., 2009). The first occurrence of this genus is *C. versteegi* from the locality of Inkonak (MN1, 'Agenian,' early Miocene) in Anatolia (de Bruijn et al., 1993). The youngest record is not clear. In the Nord Alpine Foreland Basin (NAFB), the presence in the MN9 (Vallesian, late Miocene) of *Cricetodon* sp. from Nebelberg TGL III (Prieto et al., 2010) is subject to doubtful taxonomic assignment, because it is considered to be *Hispanomys* sp. by Kälin and Kempf (2009). The allocation to the MN9 in the case of *Cricetodon* sp. from Petersbuch 14 (NAFB) and *C. albanensis* from La Parrilla and Buenaventura 3 (Duero Basin, Spain) remains uncertain according to Rummel and Kälin (2003) and Garía Moreno (1988), respectively. Excluding these occurrences, the youngest record of *Cricetodon* is *C. klariankae* from Felsőtárkány-Felnémet 2/3 and 2/7 (MN7/8, Aragonian, middle Miocene) in the Felsőtárkány Basin, Hungary (Hír, 2007).

The taxonomic status of some species attributed to *Cricetodon* has been problematic. This is because *Cricetodon* is one of the first described fossil small-mammal genera and the diagnosis proposed by Lartet (1851) presents very inclusive criteria. Therefore, a large number of European species have been accommodated within this genus. Some of them are now included in genera belonging to different Cricetidae tribes such as *Megacricetodon*

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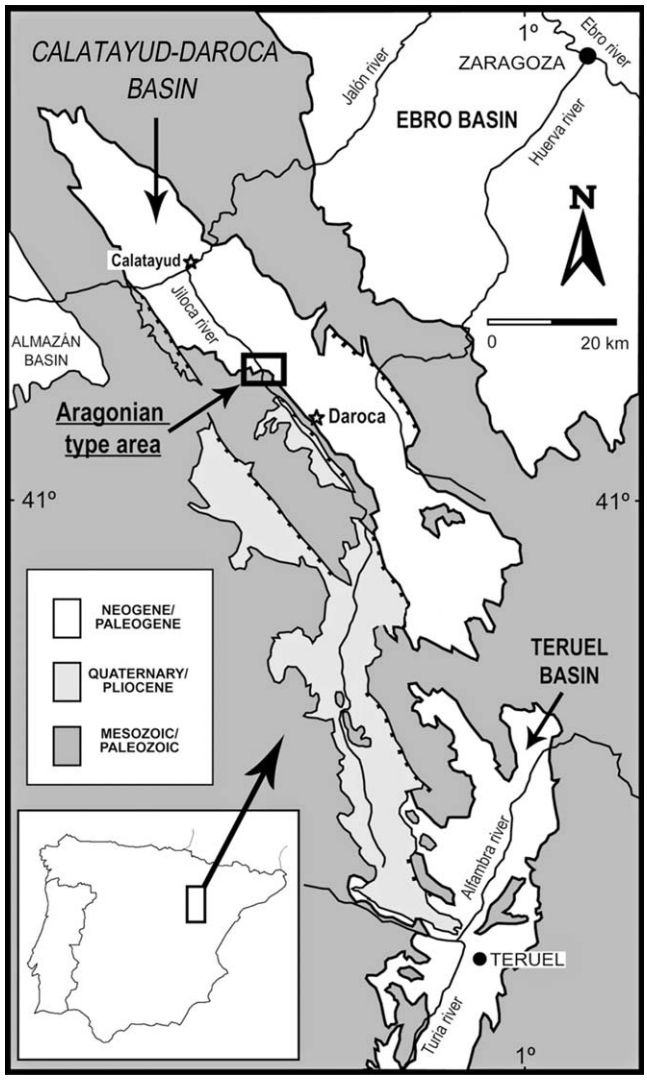


FIGURE 1. Geological map of the Calatayud-Daroca Basin. The square marks the situation of Aragonian type area. Modified after García-Paredes et al. (2010).

minor (Lartet, 1851) or *Democricetodon larteti* (Schaub, 1925).

Cricetodon is a very important genus in the biostratigraphy of the continental deposits from the middle and upper Aragonian (de Bruijn and Saraç, 1992; Daams et al., 1998, 1999a). The presence of *Cricetodon* is one of the criteria used for the definition of the local biozone E in Calatayud-Daroca and Madrid basins (van der Meulen et al., 2011, 2012). The systematics and evolution of these cricetids is not clear, despite the significant research carried out in the past, and the taxonomic status of *Cricetodon* has changed through time (i.e., Freudenthal, 1966; Mein and Freudenthal, 1971a, 1971b). The first studies of the genus in the Calatayud-Daroca Basin were made by Freudenthal (1963, 1966). He described several species and proposed the first phylogeny of *Cricetodon*. This first approach was later improved by the work of Mein and Freudenthal (1971a, 1971b) in which most of species of this genus were described in detail. Mein and Freudenthal (1971a) emended the original diagnosis of *Cricetodon* made by Lartet in 1851. Additionally, they proposed four new subgenera within it: *Hispanomys*, *Ruscinomys*, *Pseudoruscinomys*, and *Cricetodon.* Because this emended diagnosis refers simultaneously to the four subgenera, when van der Weerd (1976) erected *Hispanomys* and *Ruscinomys* as genera and synonymized *Pseudoruscinomys*, the proposed diagnosis for the subgenus by Mein and Freudenthal (1971a) should be considered as generic. Since then, the most recent emended diagnosis of *Cricetodon* has been proposed by de Bruijn et al. (1993), being widely accepted and the most used to date. As a result of the aforementioned taxonomic status changes and the fact that the limits between these genera are not clear enough, some species originally included within the genus *Cricetodon* have been placed in other Cricetodontini genera; that is the case, for example, of *Hispanomys aguirrei* (Sesé, 1977), *H. lavocati* (Freudenthal, 1966), and *H. lusitanicus* (Schaub, 1925).

Regarding the species from the biozone E in the Calatayud-Daroca Basin, de Bruijn et al. (1993) pointed out that the material present in Las Umbrías 11 (previously named as Las Planas 5A2) and the remains of Las Planas 4A and 4B suggest a new species of *Cricetodon.* Despite these preliminary conclusions and the new material discovered since then, the remains of *Cricetodon* from the biozone E of Las Umbrías and Las Planas sections have neither been completely described nor assigned to particular species until the present paper.

Different authors have focused on the study of the faunas of Cricetodontini from other regions, e.g., Anatolia in Turkey, and their relationship with the oldest cricetid records in Europe (Sen and Ünay, 1979; Klein Hofmeijer and de Bruijn, 1988; de Bruijn et al., 1993; de Bruijn and Ünay, 1996; Rummel, 1998). The efforts of the micromammal researchers of the Calatayud-Daroca Basin have been focused on the *Cricetodon* representatives from younger localities (Álvarez-Sierra et al., 2003; López-Guerrero et al., 2009); however, it is important to understand the first record of Cricetodontini from Calatayud-Daroca in order to complete the revision of the whole middle Miocene rodent faunas from this basin that is currently in progress (López-Guerrero et al., 2007, 2008).

Therefore, the main aims of this study are to characterize the first representatives of *Cricetodon* in the Aragonian type area through morphological and metrical analysis of the cheek teeth, to specify their stratigraphic distribution during the middle Aragonian, and to compare them morphometrically with other representatives of the genus present in Europe and Asia Minor.

MATERIALS AND METHODS

This study includes a morphological and metrical analysis of 52 cheek teeth of *Cricetodon* from the Calatayud-Daroca Basin. Table 1 shows the different localities studied, the number of molars examined, and the abbreviations used throughout this paper. The anatomical abbreviations for upper molars are M1, M2, and M3 and for lower molars, m1, m2, and m3. The studied material belongs to eight localities spanning a time interval from 14.06 to 13.80 Ma (van Dam et al., 2006). In addition, we revised material of *C. soriae* from the type locality Somosaguas N (Madrid Basin) stored at the Universidad Complutense de Madrid, Madrid (Spain); the type material of *C. bolligeri* from Petersbuch 10 stored at Bayerische Staatssammlung für Paläontologie und Geologie, Munich (Germany); *C. sansaniensis* from the type locality of Sansan stored at the Muséum d'Histoire Naturelle de Bâle, Basle (Switzerland); the type material of *C. aureus* and *C. meini* from Vieux-Collonges and *C. albanensis* from La Grive–Saint Alban stored at the Nederlands Centrum voor Biodiversiteit-Naturalis (NCB-Naturalis), Leiden (The Netherlands); and finally, *C. jotae* from its type locality, Manchones, stored at the Instituut voor Aardwetenschappen, Utrecht University, Utrecht (The Netherlands). The remaining species of

TABLE 1. *Cricetodon soriae* specimens from the Calatayud-Daroca Basin.

Age (Ma)	Localitiy	Abbrevation of locality	Collection	Number studied						
				M1	M2	M3	m1	m2	m3	N
13.80	Las Umbrías 20	LUM20	MNCN	2	1	2	1		1	7
13.88	Las Planas 4C	LP4C	RGM	—	—	2	—	—	—	2
13.95	Las Umbrías 19	LUM19	MNCN	2	1	2	—	—	1	6
13.96	Las Planas 4B	LP4B	IAUU	—	—	—	—	1	1	2
—	Las Planas 4BA	LP4BA	MNCN	1	1	2	2	1	—	7
13.98	Las Planas 4A	LP4A	IAUU	—	—	—	—	1	—	1
14.04	Las Umbrías 16	LUM16	MNCN	—	—	—	1	2	2	5
14.06	Las Umbrías 11	LUM11	MNCN	2	2	1	2	4	3	14
14.10–13.80	Somosaguas N	SOMN	UCM	—	1	1	1	2	3	8

Chronological information of the studied localities: Aragonian (middle) Continental Stage; Mammal Neogene Zone (MN5) proposed by Mein (1975) for Europe and revised by de Bruijn et al. (1992); and local biostratigraphical zone (E) after Daams et al. (1999a). Numerical ages of the localities after van Dam et al. (2006). For abbreviations for the localities and institutions where the fossils are stored, see Institutional Abbreviations. **Abbreviation**: **N**, number of elements of *Cricetodon soriae* studied in each locality of Calatayud-Daroca and Madrid.

Cricetodon have been studied using data available in the published descriptions of their type localities. All the species of *Cricetodon* published to date are summarized in Table 2, including their type localities and ages.

Length and width measurements for each specimen, given in mm, have been taken using a Nikon Measuroscope 10 microscope with digital micrometer. The procedure used to measure the maximum length and width is shown in Figure 2. All the measurements, the number of measured specimens, and minimum, maximum, and mean values are given in Table 3. In order to compare the studied material with the large-sized species of *Cricetodon*, Table 4 includes measurements taken from the literature. In the case of the *C. aureus* M3, we applied our morphological criteria to separate *C. aureus* from *C. meini* and, afterwards, we recalculated the minimum, mean, and maximum values using Mein and Freudenthal (1971b) data set of the type series included in the collection database of the NCB-Naturalis.

The nomenclature used for the structures present in the occlusal surface, modified after Mein and Freudenthal (1971b), is summarized in Figure 3. The photographs were taken with an environmental scanning electron microscope FEI Quanta 200. The image processing was made using Adobe Photoshop software. The molars are figured as if they were from the right side; reversed images have been indicated by an underlined label.

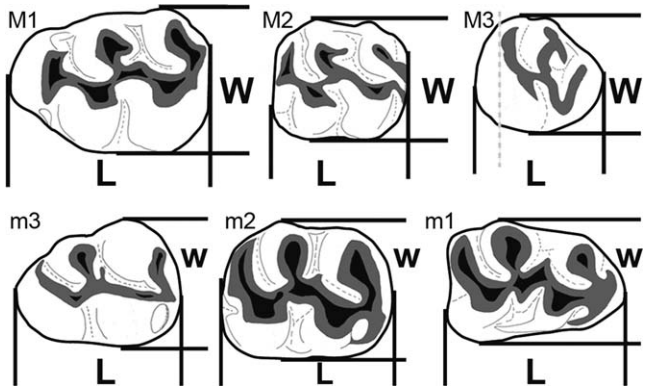


FIGURE 2. Measurement method for lengths and widths used in the present paper. The upper drawings represent left upper teeth (from M1 to M3) and the lower drawings represent right lower m3, m2, and m1. **Abbreviations**: **L**, length; **W**, width.

TABLE 2. List of the comparison species studied, type locality, and their ages.

Species	Locality	Age	Reference (for the age)
Cricetodon fandli	Gratkorn	MN7/8	Prieto et al., 2010
C. klariankae	Felsőtárkány-Felnémet 2/3	MN7/8	Hír, 2007
C. bolligeri	Petersbuch 10	MN7/8	Ziegler et al., 2005
C. jumaensis	Petersbuch 18	MN7/8	Rummel, 2001
C. cariensis	Sariçay	MN7	Sen and Ünay, 1979
C. albanensis	La Grive–Saint Alban	MN7	Mein and Freudenthal, 1971a
C. engesseri	Chräzerentobel 505m	MN7	Rummel and Kälin, 2003
C. sansaniensis	Sansan	MN6	de Bruijn et al., 1992
C. pasalarensis	Paşalar	late MN6	Peláez-Campomanes and Daams, 2002
C. jotae	Manchones	MN6, biozone G2	de Bruijn et al., 1992
C. hungaricus	Hasznos	MN6	de Bruijn et al., 1993
C. caucasicus	Belometchetskaya	late MN6	de Bruijn et al., 1992
C. soriae	Somosaguas	MN5, biozone E	Hernández-Fernández et al., 2006
C. meini	Vieux-Collonges	MN4–MN5	de Bruijn et al., 1992
C. candirensis	Çandir	MN5	de Bruijn et al., 2003
C. aureus	Vieux-Collonges	MN4–MN5	de Bruijn et al., 1992
C. volkeri	Dingshanyanchi Fm.	middle Miocene	Wu et al., 2009
C. aliveriensis	Aliveri	MN4	Klein Hofmeijer and de Bruijn, 1988
C. wanhei	Songlinzhuang	early Miocene	Qiu, 2010
C. tobieni	Horlak 1a	MN3–MN4	Tobien, 1978
C. kasapligili	Keseköy	MN3	de Bruijn et al., 1993
C. versteegi	Kilçak 3a	MN1	de Bruijn et al., 1993

TABLE 3. Lengths and widths of the upper and lower molars taken of *Cricetodon soriae* from Calatayud-Daroca.

		Length				Width				
Molar	Locality	Min	Mean	Max	N	Min	Mean	Max	N	L/W
M1	LUM19		3.16		1		2.07		1	1.53
	LUM11		3.3		1	2.13	2.14	2.14	2	1.54
M2	LUM20		2.52		1		2.3		1	1.1
	LP4BA		2.59		1		2.17		1	1.19
	LUM11		2.47		1		2.11		1	1.17
M3	LUM20	2.19	2.22	2.24	2	1.9	1.92	1.95	2	1.16
	LP4C		2.09		1		1.93		1	1.08
	LUM19		2.03		1		1.87		1	1.09
	LP4BA	1.93	1.96	1.99	2	1.88	1.94	1.99	2	1.01
	LUM11		2.24		1				1	
m1	LUM20		2.74		1		1.94		1	1.41
	LP4BA						1.71		1	
	LUM11		2.65		1		1.82		1	1.46
m2	LP4B		2.55		1		1.96		1	1.30
	LP4A						2.03		1	
	LUM16		2.38		1		1.94		1	1.23
	LUM11	2.49	2.53	2.57	3	1.93	2.04	2.14	2	1.24
m3	LUM20		2.78		1		2.2		1	1.26
	LUM19						1.98		1	
	LP4B		2.25		1		1.88		1	1.2
	LUM16	2.53	2.63	2.73	2	1.86	1.94	2.02	2	1.36
	LUM11	2.64	2.69	2.75	3	1.96	2.02	2.08	3	1.33

Measurements are in mm. **Abbreviations**: **Min**, minimum value; **Max**, maximum value; **N**, number of specimens; **L/W**, length/width index.

Institutional Abbreviations—**IAUU**, Instituut voor Aardwetenschappen, Utrecht University, Utrecht, The Netherlands; **MNCN**, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain; **RGM**, NCB-Naturalis, former Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands; **UCM**, Universidad Complutense de Madrid, Madrid, Spain.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family CRICETIDAE Fischer von Waldheim, 1817
Subfamily CRICETODONTINAE Stehlin and Schaub, 1951
Tribe CRICETODONTINI Simpson, 1945
Genus *CRICETODON* Lartet, 1851

TABLE 4. Lengths and widths of the upper and lower molars of large species of *Cricetodon*.

		Length				Width				
Molar	Species	Min	Mean	Max	N	Min	Mean	Max	N	L/W
M1	*C. klariankae*	3.30	3.39	3.55	8	2.15	2.21	2.27	9	1.53
	C. sansaniensis	2.99	3.38	3.68	34	2.00	2.19	2.35	33	1.54
	C. albanensis	3.18	3.48	3.77	50	1.99	2.15	2.31	50	1.62
	C. aureus	3.19	3.34	3.67	13	1.98	2.12	2.35	13	1.57
M2	*C. klariankae*	2.65	2.80	2.92	11	1.85	2.03	2.17	11	1.38
	C. sansaniensis	2.26	2.56	2.77	26	1.94	2.15	2.41	26	1.19
	C. albanensis	2.44	2.61	2.77	50	1.92	2.06	2.20	50	1.20
	C. aureus	2.45	2.55	2.65	8	2.01	2.09	2.18	8	1.22
M3	*C. klariankae*	1.76	1.91	2.05	11	1.62	1.76	1.90	11	1.09
	C. sansaniensis	1.91	2.09	2.31	26	1.73	1.96	2.16	23	1.07
	C. albanensis	1.94	2.11	2.30	50	1.77	1.92	2.05	50	1.1
	C. aureus	1.97	2.10	2.23	25	1.88	1.97	2.07	25	1.07
m1	*C. klariankae*	2.65	2.74	2.80	13	1.67	1.79	1.95	13	1.53
	C. soriae		2.65		1		1.86		1	1.42
	C. sansaniensis	2.59	2.86	3.08	29	1.74	1.89	2.08	29	1.51
	C. albanensis	2.70	2.94	3.20	50	1.76	1.87	1.97	50	1.57
	C. aureus	2.61	2.73	2.89	12	1.73	1.81	1.90	12	1.51
m2	*C. klariankae*	2.45	2.69	2.87	16	1.75	1.93	2.05	16	1.39
	C. soriae		2.58		1		2.05		1	1.26
	C. sansaniensis	2.55	2.71	2.89	25	1.93	2.14	2.37	32	1.27
	C. albanensis	2.45	2.65	2.86	50	1.90	2.06	22.3	50	1.29
	C. aureus	2.50	2.61	2.65	17	1,91	2.03	2.21	17	1.29
m3	*C. klariankae*	2.32	2.41	2.5	9	1.75	1.85	2	9	1.30
	C. soriae	2.37	2.5	2.64	1	2.03	2.08	2.12	2	1.20
	C. sansaniensis	2.39	2.65	3	20	1.81	2.02	2.2	20	1.31
	C. albanensis	2.49	2.64	2.8	50	1.85	1.98	2.1	50	1.25
	C. aureus	2.19	?	2.77	7	1.75	?	2.16	7	

Measurements are in mm. Measurements for *C. sansaniensis*, *C. klariankae*, and *C. albanensis* and the M1, M2, m1, m2, and m3 of *C. aureus* and *C. soriae* from SOMN were given by Maridet and Sen, in press; Hír, 2007; Mein and Freudenthal, 1971a, 1971b; and Hernández Fernández et al., 2006. Descriptive statistics presented for M3 of *C. aureus* were calculated using the data set of the type series included in the collection database of the NCB-Naturalis, Leiden (The Netherlands), applying the new criteria of the present paper to classify the M3. **Abbreviations**: **Min**, minimum value; **Max**, maximum value; **N**, number of specimens; **L/W**, length/width index.

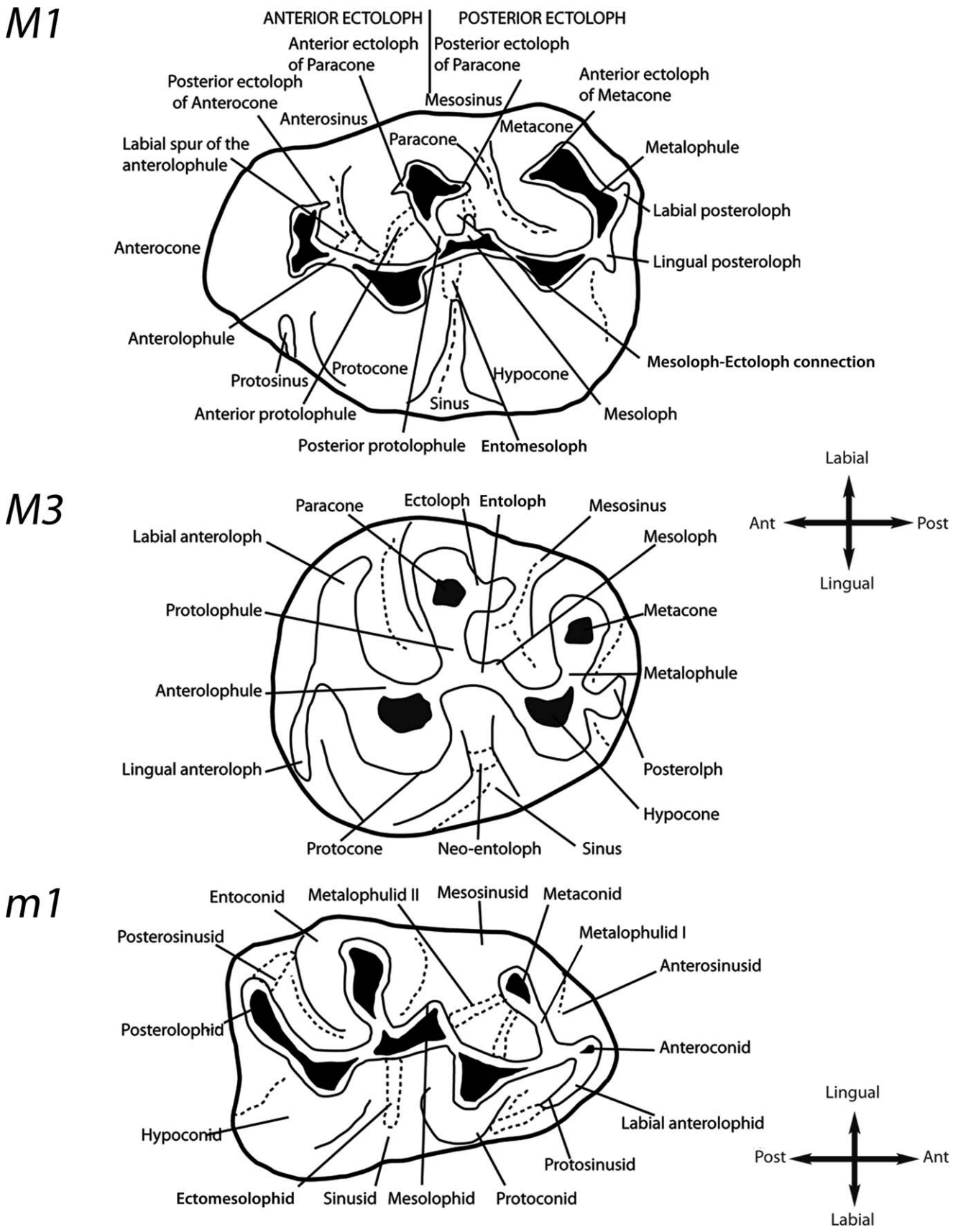


FIGURE 3. Terminology of the parts of the cheek teeth of *Cricetodon*. Only the M1, M3, and m1 morphologies have been drawn; however, the nomenclature can be applied to the rest of the upper and lower molars. Modified after Mein and Freudenthal (1971b).

Original Diagnosis—"[Rodents with tubercular cheek teeth. Same tooth pattern and number of teeth as rats: six for each mandible. Molars present fewer tubercles than those of domestic rats. They are more related to the molars of the hamsters. However, they differ from the latter by the presence of an additional tubercle when the first upper and lower molars are considered. The most significant similarity with hamsters concerns the presence of an arterial opening on the exterior condyle of the humerus that is absent in the case of domestic rats]" (Lartet, 1851:20; translated from French).

Emended Diagnosis—"[Medium- to large-sized Cricetodontini, the upper incisors are smooth or lined by a 'dipodoid' type groove. The M1 has four or five roots, the posterior root of m2 can be simple or bifurcate; the M1 has a simple or bifurcate anterocone, the upper molars show a trend in developing ectolophs; the M1 often shows protostyls and parastyls; lower molars often have protostylids, ectostylids, and ectomesolophids; the m1 always has a descending labial ridge from the higher part of the anteroconid; molars are brachyodonts or hypsodonts, but the height of the crown of an unworn tooth never exceeds the length of the roots of a worn teeth]" (Mein and Freudenthal, 1971a:17; translated from French).

Remarks—As explained in the Introduction, this emended diagnosis refers simultaneously to the subgenera *Hispanomys*, *Ruscinomys*, *Pseudoruscinomys*, and *Cricetodon* sensu Mein and Freudenthal (1971a).

Diagnosis for the Subgenus—"[Medium to large-sized Cricetodontini, the upper incisors are smooth, the ectolophs of the upper molars are absent or weak; the molars are brachyodont; the anterocone on the upper M1 is simple or bifid; the upper M1 has four roots; the lower m2 has two or three]" (Mein and Freudenthal, 1971a:17; translated from French).

Emended Diagnosis—"Small, medium or large-sized Cricetodontinae with low-crowned cheek teeth. Cusps of cheek teeth 'inflated'. Anteroconid of m1 bearing a small rounded cusp. Majority of the m1 with double metalophulid or metalophulid II only. Anterocone of M1 single or double. Labial branch of the anterolophid of the m2 incorporated in the metalophulid I. The M1 and M2 with three or four roots. Free posterior arm of the hypoconid absent in all lower molars. Occlusal surface of all cheek teeth worn flat in senile specimens" (de Bruijn et al., 1993:177).

Type Species—*Cricetodon sansaniensis* Lartet, 1851.

Other Species Included—See Table 2.

CRICETODON SORIAE López Martínez, Cárdaba, Salesa, Hernández Fernández, Cuevas González, and Fesharaki, 2006 in Hernández Fernández et al., 2006.

(Figs. 1–7; Tables 1 and 3)

Cricetodon soriae n. sp. López Martínez, Cárdaba, Salesa, Hernández Fernández, Cuevas González, and Fesharaki, 2006, in Hernández Fernández et al., 2006:275, figs. 10–11 (original description).

Cricetodon meini Freudenthal, 1963:74 (only for Las Planas 4A and 4B).

Cricetodon n. sp. 3 in de Bruijn, Fahlbusch, Saraç and Ünay, 1993:206, pl. 17.

Original Type Locality—Somosaguas N (SOMN), Madrid Basin, Spain.

New Localities—See Table 1.

Stratigraphic Range—Middle Miocene (middle Aragonian, upper part of the MN5, local biozone E).

Geographical Range—Central basins of the Iberian Peninsula.

Original Diagnosis—"[Medium-sized *Cricetodon*, with a relatively short and wide m1 and a relatively developed m3; reduced ectoloph, mesoloph, and mesolophid; posterior metalophid in m1. It differs from *C. aureus* by the dental proportions and its smaller size; it differs from *C. jotae* by its more robust m1, the posterior metalophid in the m1, less development of the ectoloph on the M2, the larger absolute width in all elements, and the larger absolute and relative size of M2, m2, and m3]" (López Martínez, Cárdaba, Salesa, Hernández Fernández, Cuevas González, and Fesharaki, 2006 in Hernández Fernández et al., 2006:275; translated from Spanish).

Emended Diagnosis—Medium- to large-sized *Cricetodon*. Upper and lower molars without styls or stylids. M1 with anterior and posterior protolophule; anterior ectoloph on the M1 absent. Anterior ectoloph on the M2 is weak and it can be observed as an enamel spur; posterior ectoloph well distinguished and short, never connected to the paracone. High-crowned M3 with a short and disconnected posteroloph; well-developed hypocone; neoentoloph hardly developed or absent; and with a continuous entoloph. Short and wide m1; metalophulid I always present, may be disconnected; metalophulid II always present. The lower third molar is large and longer than the m1; the length m1/length m3 index is more or less 1; variable mesolophid on the m3, it may be short and connected to the metaconid, long and connected either to the metaconid or to the entoconid, or double connected to both the metaconid and the entoconid.

Differential Diagnosis—*Cricetodon soriae* differs from *C. aureus* Mein and Freudenthal, 1971b, in: larger size of the m3; more developed hypocone and greater degree of hypsodonty on the M3; lack metalophulid I on the m1; presence of entoconid spur on the m1. Differs from *C. caucasicus* Argyropulo, 1938, *C. kasapligili* de Bruijn, Fahlbusch, Saraç, and Ünay, 1993, and *C. tobieni* de Bruijn, Fahlbusch, Saraç, and Ünay, 1993, in: split anterocone; four-rooted M1; larger size. Differs from *C. sansaniensis* Lartet, 1851, in: deeply split anterocone and double protolophule. Differs from *C. versteegi* de Bruijn, Fahlbusch, Saraç, and Ünay, 1993, in: less-developed anterolophs and ectolophs; larger size. Differs from *C. aliveriensis* Klein Hofmeijer and de Bruijn, 1988, and *C. pasalarensis* (Tobien, 1978) in: larger size. Differs from *C. meini* Freudenthal, 1963, in: larger size; m1 with metalophulids type I and type II always present together on the same specimen. Differs from *C. albanensis* Mein and Freudenthal, 1971a, *C. bolligeri* Rummel, 1995, *C. jumaensis* Rummel, 2001, and *C. engeseri* Rummel and Kälin, 2003, in: m1 with metalophulids type I and type II always present together on the same specimen. Differs from *C. jumaensis* Rummel, 2001, and *C. bolligeri* Rummel, 1995, in: absence of styls on the M1. Differs from *C. candirensis* (Tobien, 1978) and *C. hungaricus* (Kordos, 1986) in: less-developed anterolophs and ectolophs. Differs from *C. cariensis* (Sen and Ünay, 1979) in: absence of enamel-coated valleys on the upper molars; ectolophs more developed. Differs from *C. jotae* Mein and Freudenthal, 1971a, in: the larger size; m1 with metalophulids type I and type II always present together on the same specimen; less-developed anterolophs and ectolophs. Differs from *C. klariankae* Hír, 2007, in: the less-developed ectolophs. Differs from '*Cricetodon*' *fandli* Prieto, Böhme, and Gross, 2010, in: the less-developed ectolophs; absence of lingual spur of the anterolophule.

CRICETODON SORIAE FROM CALATAYUD-DAROCA BASIN

Description of the Studied Material

M1—Material: LUM11 (number of specimens: 2); LP4BA (1); LUM19 (2); LUM20 (2). This molar has four roots. The tooth is very wide and short, having a rounded outline. A shallow groove on the anterior wall divides the anterocone into two parts. The

connection between the protocone and anterocone is through the anterolophule. This lophule can be present as an enlargement of the enamel. A posterior protolophule connects the paracone with the posterior branch of the protocone. An anterior protolophule connects the paracone with the anterolophule in most cases; it is absent only in LP4BA and LUM20. The anterior ectoloph is absent. The posterior ectoloph is simple, never complete. The mesoloph is short in LUM11 and LUM19, and it is incipient in LUM20. The mesoloph-ectoloph connection is absent. The metalophule is directed backwards. The labial posteroloph is quite thin but well delimited. The lingual posteroloph is absent. The anterosinus is closed by either a cingulum (LUM11) or two ridges attached to the protocone and the hypocone, respectively (LUM19). The protosinus and the mesosinus are closed by a cingulum. The sinus is either open (one out of two specimens in LUM20) or closed by a cingulum, but never by a styl. The enamel on the base of the protocone and the hypocone is rough (Fig. 4).

M2—Material: LUM11 (2); LP4BA (1); LUM19 (1); LUM20 (1). The tooth has four roots. It is short and wide, but with an outline more rectangular than in the M1. The anterocone is reduced to an enlargement of the enamel on the anteroloph. The loph that connects the anteroloph with the paracone is reduced and generally lower than the anteroloph (LUM19 and LUM20). This loph can be absent (LUM11 and LP4BA). The posterior ectoloph is simple and disconnected. Only a few specimens present mesoloph and it is short (LUM11) or incipient (LP4BA). It shows neither enamel coated valley nor an entomesoloph. Both labial and lingual posterolophs are present but weak. The anterosinus is always closed. The protosinus is well developed and it is closed by a cingulum in most specimens, although in one case (LUM20)

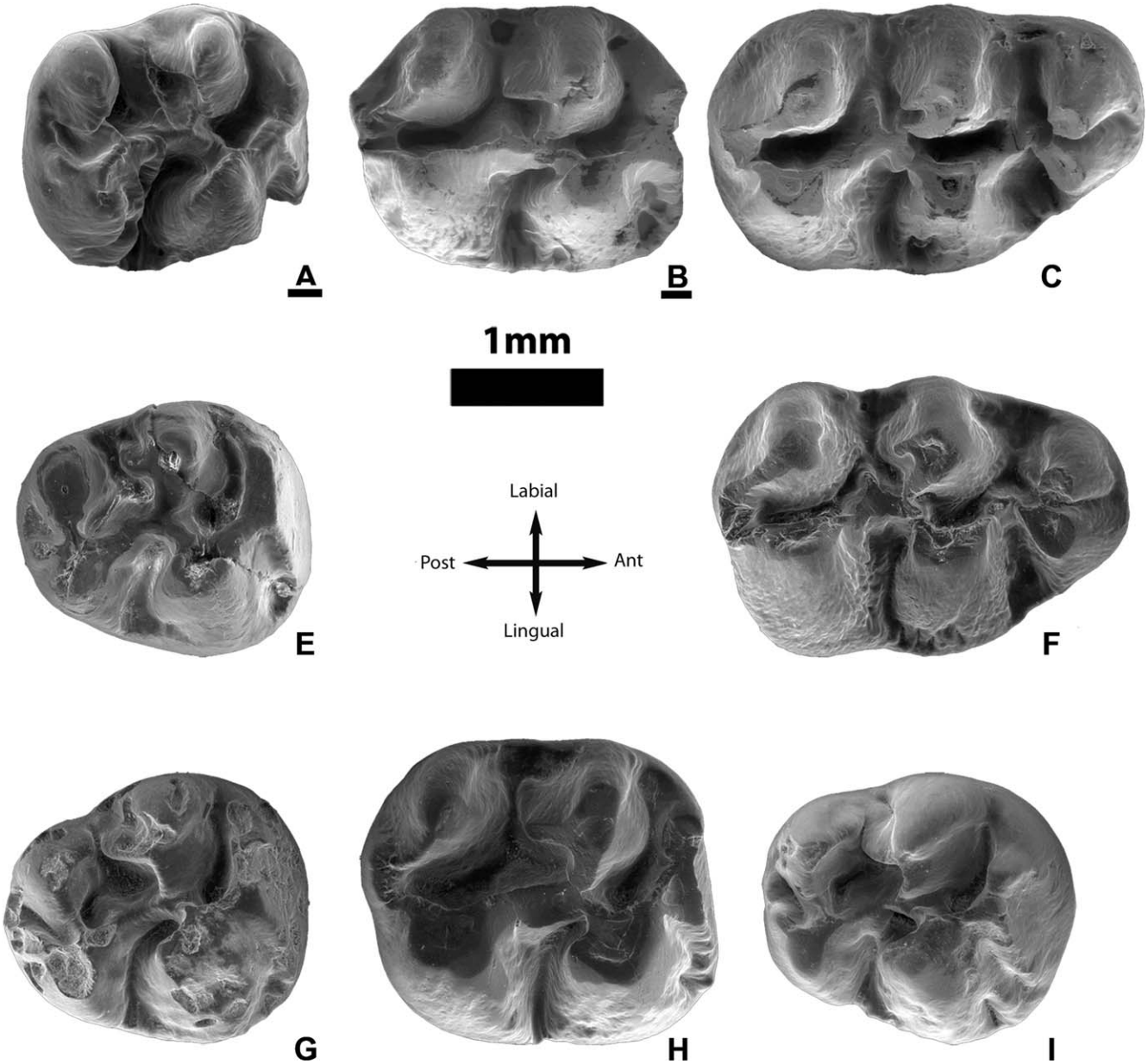


FIGURE 4. *Cricetodon soriae*, from Calatayud-Daroca. Upper molars. Las Umbrías 11: **A**, inverted left M3, LUM11-321; **B**, inverted left M2, LUM11-3; **C**, right M1, LUM11-1. Las Umbrías 19: **E**, right M3, LUM19-212; **F**, right M1, LUM19-209. Las Umbrías 20: **G**, right M3, LUM20-221; **H**, right M2, LUM20-224; **I**, right M3, LUM20-222. Scale bar equals 1 mm.

it is closed by a styl. The mesosinus, which is well developed, can be closed, either by a cingulum (LUM11, LP4BA, one out of two specimens in LUM19, and LUM20) or by two ridges (one out of two specimens in LUM19), but never by a styl. The sinus can be either open (LP4BA and LUM20) or closed by a cingulum (LUM11) (Fig. 4).

M3—Material: LUM11 (1); LP4BA (2); LUM19 (2); LP4C (2); LUM20 (2). It has a subtriangular and rounded outline with three roots. Both labial and lingual anterolophs are present, but the lingual branch is weaker than the labial one. The anterior ectoloph is absent. The posterior ectoloph can be simple (LUM11, LP4BA, LUM19, and one out of two specimens in LP4C) or double (one out of two specimens in LP4C and LUM20). It is never complete. Most of the specimens have a mesoloph and its length is variable. It may be short (one out of two specimens in LP4BA and one out of two specimens in LUM20), medium length, about half the distance between longitudinal ridge and labial border (LUM11), or long, reaching the labial border (LP4C). The mesoloph-ectoloph connection is absent. The entoloph is continuous and there is no trace of the neo-entoloph. The labial posteroloph is usually well developed but short and it never connects to the metalophule or the metacone. It is absent in only one specimen from LP4C. The sinus is anterior or transversal (LUM11) (Fig. 4).

m1—Material: LUM11 (2); LUM16 (1); LP4BA (2); LUM20 (1). This molar has an elongated shape and two roots. The anteroconid is situated on the longitudinal axis of the occlusal surface. The labial anterolophid is a well-developed ridge that connects the anteroconid with the protoconid in some specimens (LUM11 and LUM16); in the rest (LP4BA and LUM20) this ridge does not reach the protoconid. The lingual anterolophid is present in only one specimen (LUM16). In all cases, both metalophulids I and II are present together on the same specimen. The longitudinal ridge bears a mesolophid. This mesolophid can be short (LUM16 and one out of two specimens in LP4BA) or incipient. The ectomesolophid is present in only one specimen from LUM11. The entoconid spur is absent. The labial posterolophid is well developed (LUM11) or it can be absent (LUM20). The posterolophid is an oval cusp rather than a ridge, due to a constriction on the posterior wall. A low cingular ridge blocks the mesosinusid in one case (LP4BA), but in the rest, this valley is open. The sinusid is directed forwards and it can be blocked either by a cingular ridge (LUM11 and LP4BA) or by two ridges (LUM20), but never by a stylid. The posterosinusid is blocked by a cingular ridge. The protoconid and the hypoconid show rough enamel (Fig. 5).

m2—Material: LUM11 (4); LUM16 (3); LP4A (1); LP4BA (1); LP4B (1). The molar is almost rectangular in shape and the anterior and the posterior parts have similar width. The labial branch of the anterolophid is well developed. The lingual anterolophid is absent. The mesolophid is variable in length; it can be short (LP4A, LP4BA, and LP4B) or long (one out of three specimens in LUM11), but it never reaches the lingual border; in some cases (two out of three specimens in LUM11, LUM16, LP4BA, LP4B), the mesolophid is curved and projected towards the metaconid, reaching it. The lingual posterolophid is constricted behind the hypocone; its lingual part is cuspidate. The ectomesolophid is present in one case from LUM11. There is no anterosinusid and the mesosinusid is blocked by a cingular ridge in most cases, although it can also be open (one out of two specimens in LUM11 and one out of two specimens in LUM16). In most teeth, a cingular ridge is connecting the hypoconid with the protoconid at the labial border of the sinusid, whereas in one specimen from LUM11 the cingular ridge starts from the protoconid and it does not reach the hypoconid. The sinusid is never blocked by a stylid. A weak labial posterosinusid is formed on the posterior wall of the hypoconid. The lingual posterosinusid is equally blocked by a cingular ridge (LUM11 and LUM16) or by the structure resulting from the fusion of the lingual posterolophid and the entoconid (LP4A, LP4BA, and LP4B). The enamel is rough on the base of the hypoconid and the protoconid (Fig. 5).

m3—Material: LUM11 (3); LUM16 (2); LP4B (1); LUM19 (1); LUM20 (1). This molar has a triangular but rounded outline. The labial branch of the anterolophid is long and it reaches the protoconid. The lingual branch of the anterolophid is absent. The mesolophid is always present and well developed. It may reach the lingual border (LUM11 and LUM16) or it may be of a medium length (LP4B and LUM19). In one case (LUM20), the mesolophid is short and connected to the metaconid. It can be connected both to the metaconid and to the entoconid in some cases (two out of three specimens in LUM11). The ectomesolophid is absent. The lingual posterolophid is high and extends to the entoconid. It can be somewhat constricted behind the hypoconid; its lingual part is cuspidate and a weak valley on the posterior wall of the tooth is developed. The hypolophulid, which is transversal, can be connected to the anterior branch of the hypoconid. Some specimens have the mesolophid connected with the ectolophid (two out of three specimens in LUM11). In some cases (LUM11, LUM16, and LUM19), a low cingular ridge connects the hypoconid with the protoconid on the sinusid, but in the rest (LP4B and LUM20), the sinusid is open. It never presents stylids. The mesosinusid is open in most specimens, although in one case from LUM16 it is blocked by a low cingular ridge. This structure is also present at the end of the lingual posterosinusid. In some cases (LP4B and LUM20), the lingual posterolophid projects to the entoconid closing it. The enamel of the hypoconid and the protoconid is rough (Fig. 5).

Discussion

The most important features of the studied cricetid material are medium to large size, upper molars with three or four roots, and split anterocone on the M1. Most of the m1s have metalophulids I and II, the anteroconid bearing a small rounded cusp, and the lower molars often with ectomesolophids. These features agree with the proposed diagnosis of the genus *Cricetodon* sensu de Bruijn et al. (1993).

Furthermore, the studied material possesses features such as brachydont molars, with short or absent ectolophs that fit into the group 5 defined by Prieto et al. (2010) for Cricetodontini.

Among the Calatayud-Daroca remains, we observe differences in the degree of the development of mesolophs and mesolophids in all elements. These structures are less developed on the upper molars, where they are short or reduced to an 'incipient mesoloph' (an enlargement of the enamel on the longitudinal ridge), whereas they are more developed on the lower molars. The mesolophids can be medium or long in the material from the older localities (LUM11, LUM16), although in the youngest locality (LUM20) it can form a short crest. The posterior ectolophs on the M3 also show variability in their development. Simple ectolophs on LUM11 and LP4A that develop a second branch on LP4C and LUM20 are present.

Another type of differences is in the frequency of occurrence of the cingular ridges that are blocking the main valleys. Structures such as the cingulum that blocks the sinus and labial posteroloph on the M2 are present on the older localities (LUM11, LP4BA), whereas the youngest locality (LUM20) shows the sinus open and the labial posteroloph is absent. We suggest that the difference in frequency of particular states of characters among the localities cannot be truly evaluated, because the number of specimens in the sample is very low. This means that it is difficult to see the complete range of morphological variability of the species at a single locality. Nevertheless, differences among the most diagnostic features, such as the size and degree of the development of the ectolophs and posterolophs on the upper molars, the presence of double protolophule and short posterolophs on the M3, or the presence of both metalophulids on the m1, have not been

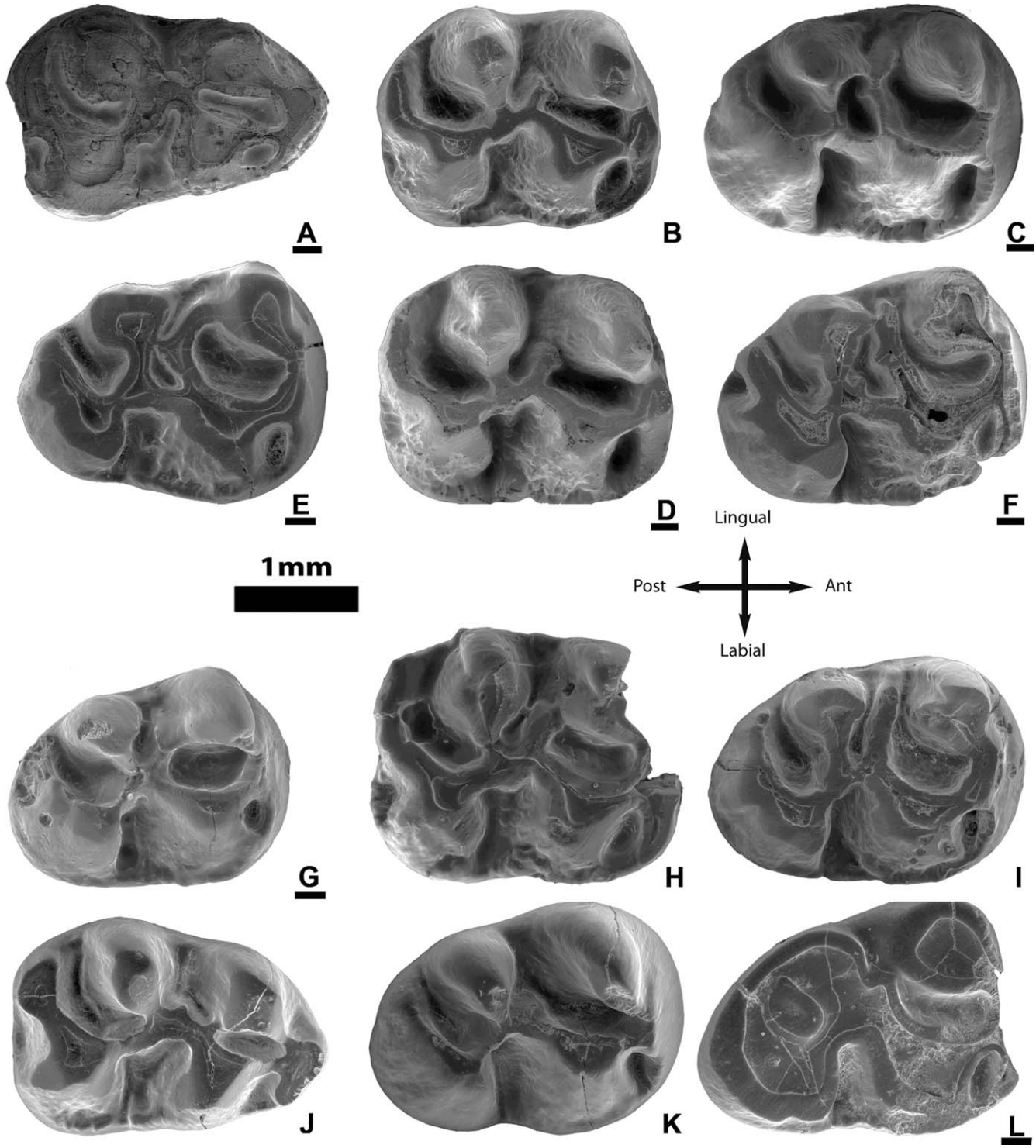


FIGURE 5. *Cricetodon soriae*, from Calatayud-Daroca. Las Umbrías 11: **A**, inverted left m1, LUM11-6; **B**, right m2, LUM11-9; **C**, inverted left m2, LUM11-4; **D**, inverted left m3, LUM11-11; **E**, inverted left m2, LUM11-10; **F**, inverted left m3, LUM11-12. Las Umbrías 16: **G**, inverted left m3, LUM16-242; **H**, right m2, LUM16-241; **I**, right m3, LUM16-243. Las Umbrías 20: **J**, right m1, LUM20-223; **K**, right m3, LUM20-225. Las Umbrías 19: **L**, inverted left m3, LUM19-214. Scale bar equals 1 mm.

found. Thus, we consider that the studied material belongs to the same species.

CRICETODON SORIAE FROM MADRID BASIN

Cricetodon soriae has been described by López Martínez et al., 2006 in Hernández Fernández et al. (2006) from the locality Somosaguas N. This site was dated around 14.1 to 13.8 Ma (Luis and Hernando, 2000), corresponding to local biozone E (middle Aragonian) from the Madrid Basin (Hernández Fernández et al., 2006; Domingo et al., 2009a). In order to clarify the morphology of the type material of *C. soriae* from Somosaguas N, we have described it under the same morphological criteria

as the material from Calatayud-Daroca. One of the paratypes, SOMN-53, was described by López Martínez et al., 2006 in Hernández Fernández et al. (2006) as an M2; however, following a comprehensive study of the material, we have identified this specimen as an M3. The different elements are not completely represented in *C. soriae* material from SOMN. The available material from the type locality corresponds to one M2, one M3, two m1s, one m2, and two m3s.

Descriptions of the Material from the Type Locality Somosaguas Norte

M2—The only available specimen presents a square-like contour. The posterior ectoloph is simple and disconnected. The specimen does not present a mesoloph. It shows neither a mesoloph-ectoloph connection nor entomesoloph. The labial posteroloph is present but weak. The anterosinus is always closed. The mesosinus and the sinus are well developed and closed by a cingulum. The sinus is curved forwards (Fig. 6).

M3—This element is represented by only one fragment. The lingual anteroloph is present. The anterior ectoloph is absent. The posterior ectoloph is simple and not complete. The mesoloph is a slight enlargement of the enamel from the longitudinal ridge. There is no enamel-coated valley. The entoloph is continuous. The labial posteroloph is present but short and it is not connected to the metalophule or to the metacone (Fig. 6).

m1—The two specimens have an elongated outline in the occlusal view. The anteroconid is situated on the longitudinal axis of the occlusal surface. The labial anterolophid is a well-developed ridge and it does not reach the protoconid. The lingual anterolophid is absent. The metalophulid I is present, but not connected to the anteroconid. The metalophulid II connects the metaconid with the posterior branch of the protoconid. The longitudinal ridge bears a slight enlargement as a short

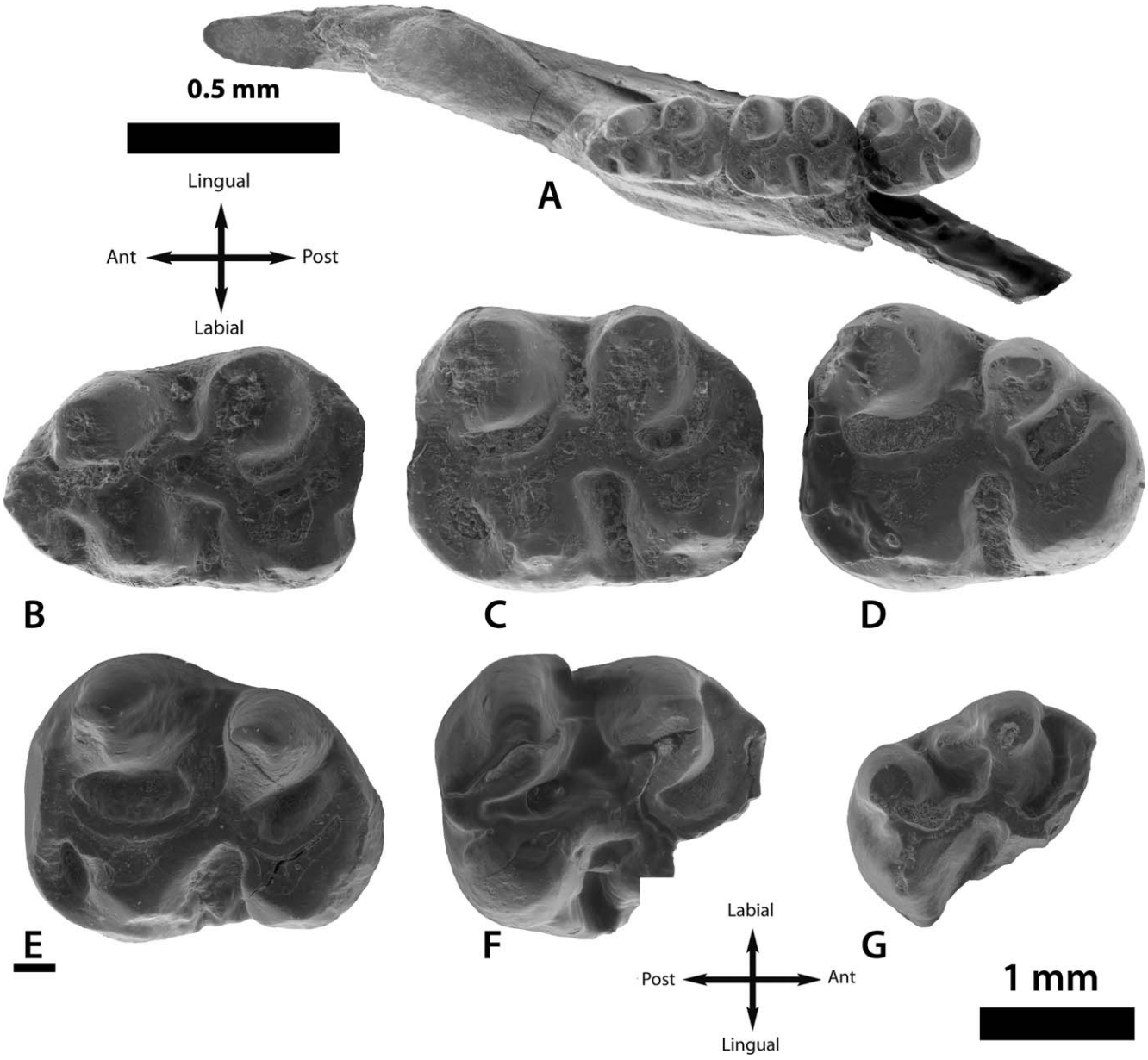


FIGURE 6. *Cricetodon soriae,* from Somosaguas N. **A**, left mandible, SOMN-2109 (holotype); **B**, left m1, SOMN-2109 (i); **C**, left m2, SOMN-2109 (ii); **D**, left m3, SOMN-2109 (iii); **E**, inverted right m3, SOMN-50; **F**, left M2, SOMN-51; **G**, left M3, SOMN-53. Scale bars equals 0.5 mm and 1 mm.

mesolophid. The ectomesolophid is absent. The entoconid is not constricted. The labial posterolophid is not present. The posterolophid is an oval cusp rather than a ridge, due to a constriction behind the hypoconid. The anterosinusid and mesosinusid are not blocked by cingulids. The sinusid is directed forwards and blocked by a cingular ridge. The posterosinusid is open (Fig. 6).

m2—The outline of the only m2 present is almost rectangular and the width of the anterior and posterior parts is similar. The labial branch of the anterolophid is well developed and reaches the protoconid. The lingual anterolophid is absent. The mesolophid is short and reaches the metaconid. The lingual posterolophid is constricted on the posterior wall. The ectomesolophid is absent. There is no anterosinusid and the mesosinusid is closed by a ridge. A cingular ridge, descending from the protoconid, blocks the sinusid. The hypoconid presents a weak labial posterosinusid. The lingual posterosinusid is closed by a cingular ridge (Fig. 6).

m3—The labial branch of the anterolophid is long, reaching the protoconid. The lingual branch of the anterolophid is present, but weak. The mesolophid is present and well developed in the two studied specimens; it never reaches the lingual border (medium length) and is connected to the metaconid. The ectomesolophid is absent. The lingual posterolophid is high and extends to the entoconid. The hypolophulid, which is transversal, can be connected to the anterior branch of the hypoconid. None of the specimens have an enamel-coated valley. The sinusid is transversal and it is either closed by a low cingulum or by a small stylid. The mesosinusid is open. There is no labial posterosinusid. A small cingular ridge is present at the end of the lingual posterosinusid (Fig. 6).

Discussion

These specimens from SOMN share several characters with the material from Calatayud-Daroca: the m1 with both metalophulids I and II present, the sinusid on the m2 closed by a cingulum, and the m2 also has a medium mesolophid that is connected to the metaconid. The M2 has no anterior ectoloph and the posterior one is simple and not connected to the metacone. But the most important similarities are present on the m3. The m3 from both SOMN and Calatayud-Daroca is large. The values of the length m1/length m3 index are between 1.02 and 1.06 for *C. soriae* from SOMN and our specimens show values of 0.99. That means that the m3 is approximately as long as the m1 in both cases.

Based on the aforementioned characters, we conclude that there are enough morphometrical criteria to assign the material from Calatayud-Daroca to *C. soriae*. Although the Madrid and Calatayud-Daroca basins show differences in the abundance of some genera (Peláez-Campomanes et al., 2003; Hernández-Ballarín et al., 2011), the similarities in their rodent assemblages have made it possible to recognize the local biozonation for Calatayud-Daroca by Daams et al. (1999a) in the Madrid Basin (Peláez-Campomanes et al., 2003). In addition, these basins have been included in the southern biogeographic province due to the similarity between the faunas of both basins (Agustí et al., 1984; Agustí, 1990; Álvarez-Sierra et al., 1990; Alberdi and Azanza, 1997; Morales et al., 1999; Gómez-Cano et al., 2011).

COMPARISON WITH OTHER SPECIES OF *CRICETODON*

As a result of this study, our knowledge about *C. soriae* has increased. This allows us to make comparisons with the other *Cricetodon* in Europe and Asia Minor.

A comparison of the measurements shows a clear difference in size between our material, and the small-sized *Cricetodon*, i.e., *C. caucasicus*, *C. versteegi*, *C. pasalarensis*, *C. aliveriensis*, *C. kasapligili*, *C. tobieni*, *C. jotae*, and *C. meini* (Argyropulo, 1938; Freudenthal, 1963; Mein and Freudenthal, 1971a, 1971b; Tobien 1978; Klein Hofmeijer and de Bruijn, 1988; de Bruijn et al., 1993; Rummel, 2001; Daxner-Höck, 2003; Markovic, 2008).

We have found several morphological differences in the species that are similar in size to *Cricetodon* from Calatayud Daroca. *Cricetodon candirensis* has upper molars with well-developed anterolophs and ectolophs (Tobien, 1978; Kordos, 1986). *Cricetodon cariensis* has enamel-coated valleys on the upper teeth, and less-developed ectolophs (Sen and Ünay, 1979) than our material. *Cricetodon bolligeri*, *C. engeseri*, and *C. albanensis* possess type I metalophulids exclusively on the m1 (Rummel, 1995; Rummel and Kälin, 2003; Kälin and Kempf, 2009), whereas metalophulid type II is always present in the material from Calatayud-Daroca. Although *C. jumaensis* presents the same kind of metalophulid (type I and II together) as *C. soriae* in the m1 (seven out of 19), metalophulids type I without type II (four out of 19) or type II alone (five out of 19) are also found in the type locality of Petersbuch 18 (Rummel, 2000, 2001). Furthermore, a styl is present on the holotype and the hypolophulid on the m3 is forward directed (Rummel, 2001), whereas *C. soriae* never have styls and the hypolophulid on the m3 is transversal.

Cricetodon sansaniensis was described by Lartet (1851) but detailed descriptions were given by Baudelot (1972). According to her descriptions, *C. sansaniensis* presents a single or weakly divided anterocone. The ectolophs in this species are absent in one half of the specimens from the type locality. However, a weak projection of the enamel in the paracone or the anterocone can be distinguished in the other half of the specimens (Baudelot, 1972; Maridet and Sen, in press). By contrast, the material from Calatayud-Daroca never shows an anterior ectoloph on the M1. *Cricetodon klariankae*, defined in Hungary, has anterior ectolophs and double posterior ectolophs on the M1, together with a reduced hypocone on the M3 (Hír, 2007). '*Cricetodon*' *fandli* presents very well developed ectolophs that reach the paracone and metacone, respectively, in the upper molars (Prieto et al., 2010).

Cricetodon soriae has been compared with the representatives of the genus from the central and eastern Europe basins that are close in age. In the Swiss Molasse of the NAFB, Uzwill-Nutzenbuech, dated at 14.9 Ma by Kälin and Kempf (2009), contains *Cricetodon* aff. *aureus*. This material shows features such as an entomesoloph and styls on the M1, but it has no anterior protolophule (Rummel and Kälin, 2003). On the German Molasse of the NAFB, the first occurrence of the genus corresponds to *Cricetodon* aff. *meini* from Eberhausen (Boon, 1991; de Bruijn et al., 1993). This fossil site is dated at 15.2 Ma by Abdul Aziz et al. (2010). This material differs from *C. soriae* such as in the presence of solely metalophulid type I and ectomesolophid on the m1 (Boon, 1991; de Bruijn et al., 1993). *Cricetodon hungaricus*, from Hasznos, Hungary (Kordos, 1986; de Bruijn et al., 1993), shows different features in comparison with *C. soriae*, such as the presence of metalophulid type II without type I, shorter mesolophids on the m3, and shorter M3 and m3 (de Bruijn et al., 1993). In Serbia, the species *C. meini* has been found in the MN6 localities of Bele Vode and Lazarevac (Markovic, 2008). The specimens present features such as absence of anterior protolophule of the M1, open valleys in the M2 and m2, styls and metalophulid type II without type I on the m1, and a reduced M3 (Markovic, 2008) that are not present in *C. soriae*. *Cricetodon meini* from Mühlbach (MN5) in Austria differs from *C. soriae* in its smaller size, it has neither anterior protolophule nor posterolophid on the M1 and it shows a reduced hypocone and paracone on the M3, and the m3 is shorter than the m1 (Daxner-Höck, 2003).

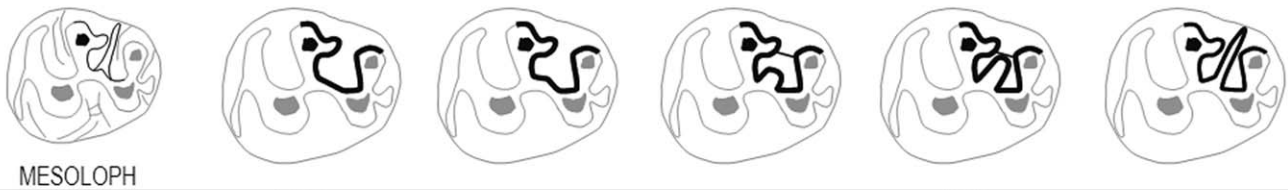
Cricetodon from Vieux-Collonges

Cricetodon aureus and *C. meini* were described in the middle Miocene French locality of Vieux-Collonges (Mein and

Freudenthal, 1971b). These authors stated that it was difficult to distinguish between the third molars of *C. aureus* and *C. meini* from Vieux-Collonges because of the large overlap in size. They studied the material stored at the Faculté des Sciences de Lyon, the Muséum d'Histoire Naturelle de Lyon, and the NCB-Naturalis. They included detailed descriptions of each element of *C. aureus* and *C. meini*. However, the metrical and morphological descriptions of the third molars were reduced to the specimens included in the maxillae and mandibles. The authors pointed out: "[We have not tried to distinguish both

NEOENTOLOPH					
LUM20	2 (100)				
LP4C	1 (100)				
LUM19	1 (50)	1 (50)			
LP4B	2(100)				
LUM11	1 (100)				
Total (*C.soriae*)	7 (87.5)	1 (12.5)			
VxC (*C.aureus*)	16 (72.7)	2 (9.1)	3 (13.6)	1 (4.5)	
VxC (*C.meini*)	66 (66.7)	21 (21.2)	12 (12.1)		

POSTEROLOPH					
M3					L/W index
LUM20	2 (100)				1.12; 1.18
LP4C	1 (100)				1.08
LUM19	2 (100)				1.09
LP4B	1(50)			1(50)	1.04:0.97
LUM11		1 (100)			
Total (*C.soriae*)	6 (75)	1 (12.5)		1(12.5)	
VxC (*C.aureus*)	10 (45.5)	3 (13.6)	2 (9.1)	7 (31.8)	1.07 (Mean)
VxC (*C.meini*)	26 (26.5)	26 (26.5)	25 (25.5)	21 (21.4)	1.06 (Mean)



MESOLOPH					
LUM20	1 (50)			1(50)	
LP4C					1 (100)
LUM19	2 (100)				
LP4B	1(50)	1(50)			
LUM11					1 (100)
Total (*C.soriae*)	4 (50)	1(12.5)		1 (12.5)	2 (25)
VxC (*C.aureus*)		2 (9.1)		6 (27.3)	14 (63.6)
VxC (*C.meini*)			2 (2.1)	25 (25.8)	70 (72.2)

FIGURE 7. Frequency and percentage (in parentheses) of the character states described for the M3 of *C. soriae* from the middle Aragonian of the Calatayud-Daroca Basin in comparison with *C. aureus* and *C. meini* from Vieux-Collonges.

forms on the third molars. We have only a few specimens on the mandible and maxilla that we know for sure is *C. aureus*]" (Mein and Freudenthal, 1971b:26; translated from French) and "[We have not given the minimum for the third molars because of the difficulty of distinguishing the specimens of both species]" (Mein and Freudenthal, 1971b:27; translated from French).

As we have pointed out before, in the discussion of the material from SOMN, we consider that the morphometric features of the third molar have a high diagnostic value in *C. soriae*. First and second molars of *C. meini* are clearly smaller than *C. soriae*, whereas *C. aureus* is closer in size to *C. soriae* (Table 4). In order to evaluate the differences in size and morphology between the *C. aureus* and *C. soriae*, we have carried out a morphometric analysis of 137 M3 elements identified as either *C. aureus* or *C. meini* stored at the RGM. Descriptive statistics presented on Table 4 for the M3 of *C. aureus* were calculated using the original measurements of Mein and Freudenthal (1971b) from the database of the NCB-Naturalis collections, but using the new specific assignation for the M3 based on the morphological criteria explained in this paper. The observed differences of the morphology of *C. aureus*, including the upper third molar, are discussed here. The frequency and percentage of the most diagnostic features are presented on Figure 7.

In general, *C. aureus* presents the following features: absent entomesoloph on the M1; some M2s with styls and complete posterior ectolophs; ectomesolophid on the m1, with some m1s displaying exclusively type I or type II metalophulid; stylids on the m2; and lingual anterolophid on the m3 (Mein and Freudenthal, 1971b) that are absent in *C. soriae*. Moreover, the mesolophs and mesolophids present in *C. aureus* are longer than the ones from Calatayud-Daroca material. The lower third molar shows a single short mesolophid that is never connected either to the metaconid or the entoconid, whereas *C. soriae* shows a long mesolophid that can be connected to either one of these cusps or to both. Our analysis determined that the degree of hypsodonty in LUM11 is approximately 1.66 mm and about 1.20–1.30 mm in *C. aureus*. The M3 of *C. aureus* is smaller and less hypsodont than the specimens from Calatayud-Daroca. In addition, we observe that the neo-entoloph is absent in all the specimens (n = 9) of *C. soriae* from Calatayud-Daroca, whereas six out 22 specimens of *C. aureus* show enamel spurs on both hypocone and protocone. This neo-entoloph can be disconnected (Fig. 7).

Regarding the posteroloph of the M3, we have described four character states for this structure: absent, short, connected to the metalophule, and connected to the metacone with absent metalophule. Most of the M3s of *C. soriae* (87.5%) show a short posteroloph, a deep valley (posterosinus) delimited by a metalophule, and a posteroloph is present. The M3 of *C. aureus* presents a short posteroloph in 45.5% of the specimens, although this ridge is absent in 31.8% of the specimens. Furthermore, the posterosinus is not as deep as in the specimens from Spain (Fig. 7). In general, the mesolophs in *C. soriae* are less developed than in *C. aureus.* The M3 of *C. soriae* presents a well-developed hypocone and thus the posterior part of the teeth is elongated. On the other hand, *C. aureus* shows a more reduced hypocone, with a posterior part of its M3 also reduced.

Sarica-Filoreau (2002) proposed that the shape of the M3 can be expressed in terms of the length/width index. She recognized two groups: (1) rounded: length/width index between 1.00 and 1.10 and (2) elongated: length/width index between 1.10–1.20. For the Calatayud-Daroca material, most (five out of seven specimens) of the values for length/width index are approximately 1.10 (Fig. 7), which means that the external outline is close to an elongated form (Figs. 4–6). In the case of *C. aureus*, the specimens show a large dispersion of index values (0.98–1.15), although we note that most of the specimens (16 out of 25) have an index of between 0.98 and 1.09. These specimens are characterized by having a rounded shape.

FINAL REMARKS

The oldest occurrence of *C. soriae* in the Calatayud-Daroca Basin is LUM11. As we pointed out above, de Bruijn et al. (1993) suggested the possibility of a new species in LUM11. The reasons they give to justify their proposal were the intermediate size between the large species–*C. aureus* and *C. sansaniensis*–and the smaller species–*C. meini* and *C. jotae*; the low degree of hypsodonty; and the combination of two features: the double protolophule and the lack of the anterior ectoloph on the M1.

After our morphological analysis of *C. soriae*, we can complete the information about the most important features of this species; these are absence of styls and stylids; low development of the mesolophids; presence of anterior and posterior protolophules on the M1; absence of the anterior ectoloph on the M1 and M3; well-developed posteroloph on the M3; presence of a metalophulid II or I and II together; presence of incomplete metalophulid I; the m3 longer than the m1; the large size of the m3; and long and double mesolophids on the m3.

Based partly of these aforementioned characters, we observe that there is a morphometric similarity between *C. soriae* and the species of *Cricetodon* from Anatolia. This idea is in agreement with the hypothesis of de Bruin et al. (1993) who suggest that the species present in LUM11 and in LP4A and LP4B may be related to the Anatolian species of *Cricetodon*. They supported that hypothesis based on a number of features, such as the presence of anterior protolophule on the M1 and the fact that the m3 is longer than the m1. Furthermore, we find it relevant to add to these common features the presence of an incomplete metalophulid I on the m1 that we described in *C. soriae*. Moreover, de Bruijn et al. (1993) observed an incomplete metalophulid I on the m1 on the species from Anatolia such as *C. versteegi* and *C. tobieni*.

It is worth noting that any further study on *Cricetodon* must include a cladistic study in order to evaluate whether *C. soriae* share a common ancestry with the species from Asia Minor, because, e.g., the phylogenetic study by Bi (2005) did not include a number of species, *C. soriae* among them.

The first occurrence of *C. soriae* is coincident with the faunal dispersion event called *Conohyus/Pliopitechus* described approximately 14 Ma ago (van der Made, 1999). Several studies indicate the initiation of an episode of global cooling and aridity (Zachos et al., 2001; Böhme et al., 2011) corresponding with this period of time. For the Iberian Peninsula, the paleoclimatical context corresponds to a cooling event and a decrease in the amount of precipitation (van der Meulen and Daams 1992; Domingo et al., 2009a; Böhme et al., 2011). Such changes in environmental conditions suggest that the Iberian Peninsula might be an optimum region for the establishment of *Cricetodon* representatives like *C. soriae*.

CONCLUSIONS

Both the morphological and metrical features of the studied material led us to identify it as *Cricetodon soriae*. This species is the oldest representative of the genus in the Iberian Peninsula. The number of localities containing *C. soriae* increases by eight and thus the species can be found not only in the Madrid Basin but also in Calatayud-Daroca. The metrical and morphological analysis performed here adds information about the size and morphology of the scarce material from the type locality (SOMN) and allows us to emend the diagnosis of *C. soriae.* Moreover, detailed comparisons with the rest of the species of *Cricetodon* including the first representatives of *Cricetodon* in Central and Eastern Europe have been performed here. In order to evaluate the differences with *C. aureus*, we have studied the type material of Vieux-Collonges and then identified the upper third molars as belonging to two species *C. aureus* and *C. meini*. Finally, we found several morphological features that *C. soriae* shares with

the Anatolian species of *Cricetodon*. The first occurrence of *C. soriae* is coincident with a mammal migration event across Europe. This migration could be related to an environmental change into a period of cooling and an increase in the aridity of the Iberian Peninsula.

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